# TWO NEW SPECIES OF ISCHNOTHELE FUNNELWEB SPIDERS (ARANEAE, MYGALOMORPHAE, DIPLURIDAE) FROM JAMAICA 

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#### Abstract

Based upon an analysis of patterns of variation in morphology, pigmentation, habitat, and Mysmenopsis kleptoparasites, two new species of Ischnothele from Jamaica (I. reggae and I. xera) are described. These allopatric sister species appear to have cospeciated with their respective Mysmenopsis kleptoparasite species, also each other's closest relatives. The rate of divergent evolution of the two kleptoparasite populations appears to be greater than that of the host populations, in part, we suggest, because of the kleptoparasites' shorter generation time.


## INTRODUCTION

This study is part of the first author's revisionary study of the ischnotheline funnelweb spiders, tropical diplurids with two rows of cheliceral teeth, an elongate terminal cymbial apophysis, and maxillary (but not labial) cuspules. The genus Ischnothele (Figs. 1, 2) is distributed throughout much of the American tropics and differs from the other two (Old World) ischnotheline genera (Thelechoris and Lathrothele) by the presence of spines on the male tibia I apophysis (Figs. 12-17), by the presence of an opposing protuberance on the male metatarsus I (Figs. 12-17), and by a reasonably clear demarcation between the bulb and embolus (Figs. 22, 23).

The unpublished occurrence of Ischnothele on Jamaica came to light during an examination of museum collections and prompted the first author to make a four-day visit to that island in early April of 1988 during a collecting trip to the American tropics. Collecting in Jamaica was limited to several areas in the southeastern part of the island (the source of $95 \%$ of previously collected specimens) and revealed marked geographic variation in the habitat, kleptoparasites, pigmentation, and morphology of these Ischnothele populations. Although more careful searching in this and other parts of Jamaica for additional and larger population samples will be needed to rigorously test hypotheses about Ischnothele species limits, we believe that we currently have sufficient data to postulate that there are two species of Ischnothele on Jamaica, and we hope that the presentation of such information will stimulate and guide future research. Moreover, our findings provide the first clear evidence for the kind of hostkleptoparasite cospeciation process which may be a key factor in the evolution of


Figures 1, 2.-Ischnothele reggae paratype, female body; 1, dorsal, showing abdominal pigmentation and bristles on chelicerae and carapace; 2, lateral.
the mysmenid genus Mysmenopsis (Platnick and Shadab 1978; Coyle and Meigs 1989), many species of which are kleptoparasites of diplurid spiders.

These two species of Ischnothele are endemic to Jamaica and are clearly each other's closest relatives. Of the several probable synapomorphies linking these species, two are especially distinctive: (1) spermathecae short and stalkless (or with a very short, broad vestigial stalk), and (2) embolus serrated. Two synapormorphies support the hypothesis that this species pair is most closely related to endemic species from Cuba (Ischnothele longicauda Franganillo) and Hispaniola: (1) ventral surface of male metatarsus I with distal keel, and (2) embolus short. A more complete phylogenetic analysis of all ischnotheline taxa will be presented in the forthcoming revision.

## METHODS

The quantitative characters used in this study are abbreviated and defined as follows: MC, number of cuspules on ventral surface of maxilla; ITSP and ITSR, number of spines on prolateral and retrolateral surfaces of male tarsus I, respectively; TAS, number of spines on male tibial mating apophysis; CSP and CSR, number of enciform spines on prolateral and retrolateral surfaces of male cymbial apophysis, respectively; CTP and CTR, number of cheliceral teeth in prolateral and retrolateral rows, respectively; $C D P$ and $C D R$, number of


Figures 3-6. -Photos of living specimens of Jamaican Ischnothele species, dorsal view; 3, 4, I. reggae; 3 , male holotype; 4 , female paratype; 5,6, I. xera; 5 , male holotype; 6 , female paratype. Scale $\mathrm{bar}=5 \mathrm{~mm}$.
cheliceral denticles adjacent to prolateral and retrolateral rows of teeth, respectively; PTarS, number of spines on female palpal tarsus; ITarS, number of spines on female tarsus I; CS, length of longest seta protruding from male carapace edge above coxa III; CL, carapace length; CW, carapace width; AMD, transverse diameter of left anterior median eye pupil; AMS, minimum distance


Figure 7.-Distribution of Jamaican Ischnothele species. Triangles designate collection localities for I. reggae, circles for I. xera, X's for juveniles only. Black bars designate areas where first author searched unsuccessfully for Ischnothele. Dotted line encloses area receiving over 75 inches of rainfall per year.
between anterior median eye pupils; OQW, ocular quadrangle width; SL, sternum length; SW, sternum width; IFL, ITL, IML, and ITarL, lengths of leg I femur, tibia, metatarsus, and tarsus, respectively; ITT, maximum diameter of male tibia I in retrolateral view along line perpendicular to ITL; MKP, distance along IML line from proximal end of male metatarsus $I$ to the intersection with perpendicular line passing through the prolateral keel apex; TAL, distance from disto-dorsal angle of male tibia I apophysis to base of apophysis in retrolateral view (Fig. 15); TAW, midpoint diameter of male tibia I apophysis in retrolateral view (Fig. 15); PFL and PTL, lengths of male palpal femur and tibia, respectively; PTT, maximum diameter of male palpal tibia in retrolateral view along line perpendicular to PTL; CYL, length of male cymbium (including apophysis) in prolateral view; CYAL, length of male cymbial apophysis from apex of prolateral cymbial lobe to tip of apophysis along line parallel to CYL; PL, distance from tip of embolus to most distant edge of palpal bulb (Fig. 23); PD, maximum diameter of palpal bulb (Fig. 23); ML, distance from proximalmost maxillary cuspule to tip of endite along line parallel to longitudinal axis of maxilla with ventral surface of maxilla in horizontal plane; CFL, distance along ML from proximal-most cuspule to perpendicular line that intersects distal-most cuspule; LSL1, LSL2, and LSL3, lengths of posterior lateral spinneret articles (basal, middle, and terminal article, respectively) measured along midventral line.

All appendage character states were recorded from the left appendage (unless missing, damaged, or not fully regenerated) except for ITSP, ITSR, TAS, CSP, and CSR, which were recorded from both appendages. All carapace and eye measurements were performed in dorsal view with the lateral borders of the carapace in the horizontal plane. The length of each leg article and of the palpal femur and tibia was measured in retrolateral view and equals the distance from


Figure 8.-Frequency distribution histogram of abdominal color variation in Jamaican Ischnothele species. Females designated by open squares, males by crossed squares. Figures 9-11. -Scattergrams for I. reggae (triangles) and I. xera (circles) with regression lines (values in mm); 9, males, TAW vs. TAL ( $I$. xera regression: $y=0.105 x+0.139$ ); 10 , males (open symbols) and females (closed symbols), OQW vs. CL (I. reggae regression: $\mathrm{y}=0.212 \mathrm{x}+0.253$; I. xera regression: $\mathrm{y}=0.188 \mathrm{x}+0.214$ ); 11 , females, OQW vs. LSL3 (I. reggae regression: $\mathrm{y}=0.142 \mathrm{x}+0.678$; I. xera regression: $\mathrm{y}=0.118 \mathrm{x} \times+$ 0.446 )
the proximal point of articulation to the most distodorsal point of the article (in the case of IFL the distal point of measurement is the tip of the condyle, which is sometimes slightly proximal of the most distal point of the article). PL and PD were recorded after positioning the palpal organ for a retrolateral and slightly ventral view with the bulb and embolus tip in the same horizontal plane.

Measurements were performed with a Wild M-5® stereomicroscope with $20 \times$ eyepiece lenses and an eyepiece micrometer scale. LSL1, LSL2, and LSL3 measurements are accurate to 0.076 mm ; SL (females), SW (females), ML, CFL, PFL, PTL, PTT, CYL, CYAL, PL, and PD are accurate to 0.018 mm ; AMD, AMS, OQW, TAL, and TAW are accurate to 0.009 mm ; all other measurements are accurate to 0.038 mm . All measurements are in millimeters.

Spermathecae were cleared in $85 \%$ lactic acid, viewed at $100-400 \times$ through a compound light microscope, and drawn with the aid of a drawing tube.

Table 1.--Quantitative character values for Jamaican Ischnothele males. Character abbreviations are defined in the Methods section of the text. All measurements given in millimeters. Range and mean given. ITSP, ITSR, TAS, CSP, and CSR values include data from both left and right appendages.

|  | reggae <br> $(N=2)$ | xera <br> $(N=3)$ | reggae <br> holotype | xera <br> holotype |
| :--- | :--- | :--- | :--- | :---: |
| MC | 51,67 | $39-52(44.0)$ | 67 | 39 |
| ITSP | $0-1(0.3)$ | $2-4(3.0)$ | 0,0 | 3,3 |
| ITSR | $0-2(1.3)$ | $2(2.0)$ | 1,0 | 2,2 |
| TAS | $7-9(8.5)$ | $4-7(5.8)$ | 9,7 | 4,4 |
| CSP | $0(0)$ | $0-1(0.7)$ | 0,0 | 1,1 |
| CSR | $0(0)$ | $0-1(0.7)$ | 0,0 | 1,1 |
| CL | $3.66,3.73$ | $3.54-4.20(3.97)$ | 3.73 | 4.16 |
| CW | $3.31,3.43$ | $3.16-3.73(3.53)$ | 3.43 | 3.70 |
| AMD | $0.19,0.20$ | $0.17-0.19(0.182)$ | 0.20 | 0.19 |
| AMS | $0.14,0.17$ | $0.12-0.15(0.133)$ | 0.14 | 0.12 |
| OQW | $1.06,1.06$ | $0.87-1.04(0.974)$ | 1.06 | 1.04 |
| SL | $2.04,2.08$ | $1.89-2.31(2.17)$ | 2.08 | 2.31 |
| SW | $1.58,1.73$ | $1.54-1.96(1.81)$ | 1.73 | 1.92 |
| IFL | $3.35,3.47$ | $3.16-3.70(3.52)$ | 3.35 | 3.70 |
| ITL | $2.73,2.73$ | $2.46-2.93(2.75)$ | 2.73 | 2.85 |
| ITT | $0.69,0.73$ | $0.62-0.85(0.74)$ | 0.73 | 0.85 |
| IML | $2.70,2.73$ | $2.66-3.04(2.88)$ | 2.73 | 2.93 |
| MKP | $1.08,1.08$ | $0.92-1.16(1.07)$ | 1.08 | 1.12 |
| ITarL | $2.54,2.54$ | $2.16-2.89(2.61)$ | 2.54 | 2.77 |
| TAL | $0.11,0.12$ | $0.26-0.41(0.352)$ | 0.12 | 0.41 |
| TAW | $0.23,0.27$ | $0.17-0.19(0.176)$ | 0.23 | 0.19 |
| PFL | $2.17,2.22$ | $2.07-2.48(2.33)$ | 2.17 | 2.48 |
| PTL | $1.63,1.65$ | $1.48-1.74(1.64)$ | 1.63 | 1.70 |
| PTT | $0.67,0.69$ | $0.57-0.70(0.65)$ | 0.67 | 0.70 |
| CYL | $1.48,1.55$ | $1.44-1.85(1.67)$ | 1.55 | 1.72 |
| CYAL | $0.81,0.94$ | $0.83-1.11(1.01)$ | 0.94 | 1.07 |
| PL | $0.83,0.85$ | $0.76-0.89(0.84)$ | 0.83 | 0.87 |
| PD | $0.48,0.48$ | $0.46-0.52(0.49)$ | 0.48 | 0.48 |
| LSL3 | $3.47,3.47$ | $3.70-3.85(3.77)$ | 3.47 | 3.77 |
| TAW(100)/TAL | 193,243 | $45-64(51.7)$ | 193 | 45 |
| MKP(100)/IML | 39,40 | $35-38(37.0)$ | 39 | 38 |
| OQW(100)/CL | 28,29 | $24-25(24.6)$ | 28 | 15 |
| CS(100)/CW | 14,15 | $18-22(20.6)$ | 25 |  |
|  |  |  |  |  |

Each species description is a composite of all the adult specimens examined; these sample sizes are given in Tables 1 and 2. The quantitative character values recorded in these tables are an integral part of each description. Colors are described from specimens under alcohol, illuminated by a tungsten bulb, and viewed through a stereomicroscope.

For the analysis of variation of dorsal abdominal pigmentation, three of the preserved adult specimens in good condition were carefully selected to serve as standards: one with a relatively dark abdomen, one with a relatively light abdomen, and one with pigmentation intermediate between these two. These dorsal abdominal pigmentation values are the result of the distribution of two components: 1) pigments beneath the abdominal cuticle and 2) light and dark setae. The three standards were placed side by side in order of increasing

Table 2.-Quantitative character values for Jamaican Ischnothele females. Character abbreviations are defined in the Methods section of the text. All measurements given in millimeters. Range, mean, and standard deviation given.

|  | reggae <br> $(N=23-27)$ | xera <br> $(N=6-8)$ |
| :--- | :--- | :--- |
| CTP | $6-12(8.8 \pm 1.5)$ | $8-10(9.3 \pm 0.7)$ |
| CDP | $0-3(0.6 \pm 0.8)$ | $0-4(0.9 \pm 1.4)$ |
| CTR | $9-12(10.0 \pm 0.9)$ | $7-9(8.4 \pm 0.7)$ |
| CDR | $8-18(13.1 \pm 2.9)$ | $10-16(13.8 \pm 2.5)$ |
| PTarS | $6-16(10.8 \pm 2.2)$ | $9-13(10.9 \pm 1.6)$ |
| ITarS | $2-7(4.3 \pm 1.0)$ | $5-11(6.3 \pm 2.1)$ |
| MC | $72-136(99.7 \pm 18.7)$ | $44-91(63.4 \pm 18.6)$ |
| CL | $4.14-7.49(5.45 \pm 0.82)$ | $3.12-5.97(4.86 \pm 1.02)$ |
| CW | $3.53-6.42(4.78 \pm 0.69)$ | $2.74-5.13(4.14 \pm 0.85)$ |
| AMD | $0.18-0.31(0.230 \pm 0.032)$ | $0.13-0.22(0.185 \pm 0.031)$ |
| AMS | $0.13-0.24(0.165 \pm 0.029)$ | $0.09-0.18(0.145 \pm 0.034)$ |
| OQW | $1.13-1.83(1.413 \pm 0.179)$ | $0.80-1.35(1.123 \pm 0.200)$ |
| SL | $2.15-3.80(2.87 \pm 0.39)$ | $1.72-3.05(2.58 \pm 0.50)$ |
| SW | $1.93-3.39(2.51 \pm 0.32)$ | $1.46-2.59(2.20 \pm 0.40)$ |
| ML | $1.24-2.26(1.65 \pm 0.26)$ | $0.89-1.66(1.38 \pm 0.30)$ |
| CFL | $0.47-1.24(0.78 \pm 0.19)$ | $0.35-0.91(0.61 \pm 0.19)$ |
| IFL | $3.23-5.74(4.17 \pm 0.59)$ | $2.32-4.26(3.55 \pm 0.72)$ |
| ITL | $2.28-4.03(2.93 \pm 0.41)$ | $1.60-3.08(2.52 \pm 0.54)$ |
| IML | $2.39-4.10(3.03 \pm 0.42)$ | $1.75-3.27(2.69 \pm 0.57)$ |
| ITarL | $1.48-2.36(1.87 \pm 0.23)$ | $1.10-2.01(1.65 \pm 0.33)$ |
| LSL1 | $1.44-2.96(2.06 \pm 0.32)$ | $1.60-2.36(1.98 \pm 0.25)$ |
| LSL2 | $1.29-2.89(1.84 \pm 0.32)$ | $1.37-2.28(1.90 \pm 0.30)$ |
| LSL3 | $3.95-8.13(5.44 \pm 1.08)$ | $3.72-6.69(5.90 \pm 1.12)$ |
| OQW(100)/CL | $24-27(25.9 \pm 0.9)$ | $21-26(23.3 \pm 1.3)$ |
| LSL3(100)/CL | $81-111(97.3 \pm 8.8)$ | $101-132(118.6 \pm 12.8)$ |
| OQW(100)/LSL3 | $23-32(27.1 \pm 2.9)$ | $18-24(19.6 \pm 2.4)$ |
| AMD(100)/ITarS | $3.5-9.6(5.7 \pm 1.3)$ | $1.9-3.8(3.1 \pm 0.7)$ |
| ITarS(100)/CTR | $17-67(43.4 \pm 10.5)$ | $56-157(76.6 \pm 33.5)$ |

darkness in an open petri dish of ethanol, which was illuminated by a 6 volt, 15 watt, Olympus TL stereomicroscope lamp positioned approximately 30 cm above the dish. All adult specimens were then individually placed in the dish, viewed close-up without magnification, and assigned an index of pigmentation, from 1 to 7, in the following manner: 1 -abdomen lighter than the lightest standard; 2abdomen like the lightest standard; 3-abdomen darker than the lightest standard and lighter than the intermediate standard; 4-abdomen like the intermediate standard; 5-abdomen darker than the intermediate standard and lighter than the darkest standard; 6 -abdomen like the darkest standard; 7 -abdomen darker than the darkest standard. This procedure was carried out independently by each author, using the same standards. For most specimens, both authors selected the same index. When the indices of a specimen differed by one unit, a coin toss decided the index. When the indices differed by two units (this happened for only two specimens), the mean was used as the index. Finally, if a specimen's abdomen was shrivelled and wrinkled, the index was lowered by one unit, and if an abdomen was covered by abnormal milky and glossy cuticle, its index was increased by one.

## ANALYSIS OF VARIATION

The marked geographic variation in habitat and pigmentation observed by the first author while collecting Jamacian Ischnothele indicated that there might be more than one species of Ischnothele on the island.

The Blue Mountain populations (Fig. 7) are found at elevations of 3200-5000 feet in what Asprey and Robbins (1953) call upper montane sclerophyll forest and mist forest. The only other Jamaican Ischnothele specimen from an upland region is from Burnt Hill, located at an elevation of 1700-2000 feet in the Cockpit region where the principal natural community is wet limestone forest. Both the Blue Mountain and Burnt Hill populations experience over 80 inches of rainfall and only the briefest dry season each year. In contrast, the populations west and east of Kingston (Fig. 7) are situated on the dry south coast between sea level and 500 feet elevation in cactus thorn scrub and dry limestone forest, respectively. The former population receives less than 30 inches of rain per year and the latter less than 45 inches; both experience a long dry season of six to ten months. The mesic Blue Mountain forest habitat is characterized by a dense ground layer of vegetation and soils with considerable organic matter, whereas the coastal habitats have little or no ground vegetation and a rocky, porous, dry substrate, either solid, jagged, honeycombed limestone rock with almost no humus and scattered patches of leaf litter (west of Kingston), or loose limestone rock and gravel with only small amounts of organic matter and scattered patches of leaf litter (east of Kingston).

Because of the greater density of white setae and the lighter pigmentation under the abdominal cuticle, all adults from the lowland populations west of Kingston are much lighter (very light grey) over most of their body and appendages (Figs. $5,6,8$ ) than the great majority of adults from the Blue Mountains and Burnt Hill, which are medium to dark brown (Figs. 3, 4, 8). The lowland sample from east of Kingston averages darker than the west of Kingston sample and lighter than the upland sample, and overlaps the pigmentation values of both those samples (Fig. 8).

The large habitat differences among these populations, especially between the upland and lowland populations, suggest that very different selection pressures may be acting on the different populations. The observations that 1) the coloration of each population approximates the substrate color characteristic of its habitat and 2) these spiders are often difficult to locate when they have been forced out of their webs by collectors and are on, or partly buried in, the substrate, are consistent with this hypothesis. Perhaps selection by visual predators is responsible for this color variation.

Unsuccessful searches for Ischnothele populations in two areas (see black bars in Fig. 7) of habitat intermediate in elevation, rainfall, vegetation cover, and substrate, and lying between the south coast and the backbone of the eastern mountain mass, suggest that the upland and lowland populations may be geographically isolated from each other by unsuitable habitat. These areas, along the Kingston to Newcastle road between Redlight and Mona and along the road from Port Morant to Bath and west of Bath, both provided geometrically suitable web sites (rock outcrops and earth road banks), but no Ischnothele webs were found.

An additional finding also suggests to us that the Blue Mountain population and the lowland populations of Ischnothele are geographically isolated and have diverged genetically; each of these two population clusters harbors a different species of Mysmenopsis kleptoparasite which are each other's closest relatives (Coyle and Meigs 1989).

Our analysis of morphological variation in and among the Ischnothele samples also supports this hypothesis that the two lowland populations have diverged markedly from the upland populations, although it should be noted that especially small male sample sizes limit the rigor of this test. The results of this analysis are summarized below:

Males: Among the five available males, noteworthy (discontinuous) variation was observed only in some leg I, pedipalp, and eye characters. The tibia I apophysis of the three lowland specimens is considerably longer and more sleder than that of the two upland specimens (Figs. 9, 12-17), but it is noteworthy that the east of Kingston male's apophysis (Fig. 16, 17) is not as long as those of the specimens from west of Kingston (Figs. 14, 15) and widens distally as in the upland males' apophyses (Figs. 12, 13) instead of being slightly constricted distally as in the west of Kingston specimens. Both west of Kingston males have a more prominent retrolateral metatarsal protuberance (Fig. 14) than do the east of Kingston (Fig. 16) and upland males (Fig. 12), and they also lack the ventroretrolateral spine that is present midway between this protuberance and the distal end of the metatarsus in the east of Kingston and upland males. The lowland males have more (2-4) prolateral spines on tarsus I (Fig. 19) than do the upland specimens ( $0-1$ ) (Fig. 18). The lowland males (Fig. 23) have a deeper indentation on the ventral face of the palpal organ at the bulb-embolus junction than do the upland males (Fig. 22). For the east of Kingston male, the silhouette of the retrolateral surface of the embolus in ventral view is more similar to that of the other lowland males than to the upland males (Fig. 24), but the reverse is true of the silhouette of the prolateral surface. The two prolateral spines on the pedipalp patella are much thicker in the lowland (Fig. 26) than in the upland males (Fig. 25). In the lowland males, the more proximal of these spines is especially stout and tapers abruptly to an extremely thin deciduous tip. The ocular quadrangle of the upland males is proportionally wider than that of the lowland males (Fig. 10).

Females: For all meristic and measurement characters, there is considerable overlap among the samples of the three main population clusters (Blue Mountain plus Burnt Hill; west of Kingston; and east of Kingston). The least overlap is found in CTR (Table 2); all but two upland specimens have more retrolateral cheliceral teeth than all the lowland specimens. Several ratios separate some of the population clusters (Table 2): OQW(100)/LSL3 (Fig. 11), OQW(100)/CL (Fig. 10), AMD(100)/ITarS, ITarS(100/CTR, and LSL3(100)/CL. For every one of these ratios the two lowland samples broadly overlap one another and are distinct from the upland specimens. The only quantitative character for which either lowland sample is even roughly intermediate between the other one and the upland sample is $\operatorname{AMD}(100) / \mathrm{ITarS}$, where most of the west of Kingston specimens are intermediate.

The females from west of Kingston all have distinctively low and relatively weakly sclerotized median bulbs which are much shorter than the lateral bulbs,


Figures 12-19.—Jamaican Ischnothele species, male leg I characters; 12, 13, I. reggae holotype, retrolateral; 12, tibia and metatarsus; 13, tibial apophysis; 14, 15, I. xera holotype, retrolateral; 14, tibia and metatarsus; 15, tibial apophysis; 16, 17, I. xera E. of Kingston, retrolateral; 16, tibia and metatarsus; 17, tibial apophysis; 18, 19, holotypes, tarsus, prolateral; 18, I. reggae; 19, I. xera. Scale lines: 1.0 mm for Figs. 12, 14, 16, 18, 19; 0.5 mm for Figs. 13, 15, 17.
and the secondary bulb between these two is small and not attached to the lateral bulb (or may even be missing) (Figs. 33-35). The upland females all have large, moderately heavily sclerotized median bulbs that are as tall or nearly as tall as the lateral bulbs, and the secondary bulb is usually, but not always, attached to the lateral bulb (Figs. 27-29). The spermathecal form of the specimens from east of Kingston (Figs. 30-32) is intermediate between those of these two samples, but appears closer to that of the upland sample than to the west of Kingston form.

In conclusion, the data available on variation in habitat, pigmentation, kleptoparasites, and morphology suggest that the Blue Mountain, east of Kingston, and west of Kingston populations have diverged genetically and that the latter two (lowland) have diverged less from each other than from the upland population. (The observation that the east of Kingston population is intermediate in several varying characters suggests that the three populations may be remnants of a once continuously distributed ancestral population that exhibited clinal


Figures 20-26.—Jamaican Ischnothele species male pedipalp characters; 20, 21, holotype tibia, cymbium, and palpal organ, retrolateral; 20, I. reggae; 21, I. xera; 22, 23, holotype palpal organ, ventral aspect of retrolateral; 22, I. reggae; 23, I. xera; 24, distal three-fourths of embolus, ventral view, I. reggae holotype (top), I. xera from E of Kingston (middle), I. xera paratype (bottom); 25, 26, patella, prolateral; 25, I. reggae holotype; 26, I. xera, E of Kingston. Figures 27-35.-Jamaican Ischnothele species female spermathecae; 27-31, 33-35, right side only, 32, both sides; 27-29, I. reggae; 27, Blue Mtns. 17 mi . post; 28, Whitfield Hall; 29, Catherine's Peak; 30-35, I. xera; 30-32, E of Kingston; 33-35, paratypes. Scale lines: 1.0 mm for Figs. 20, 21, 25, 26; 0.5 mm for Figs. 22-24; 0.1 mm for Figs. 27-31, 33-35; 0.2 mm for Fig. 32.
variation.) This indicates that it is more likely that intrinsic isolating mechanisms have evolved between the upland and lowland populations than between the lowland populations; consequently, we will describe two species of Jamacian Ischnothele, one from the uplands and one from the lowlands. We want to emphasize, however, that much more field work is necessary to gather enough data on geographic distribution, on variation in habitat, morphology, and other characters, and on reproductive behavior, to be able to rigourously test this and alternative hypotheses.

## COEVOLUTION

Since the two Jamaican Ischnothele species are each other's closest relatives, since each harbors a different species of Mysmenopsis kleptoparasite, and since these two Mysmenopsis species are also each other's closest relatives (Coyle and Meigs 1989), it appears that these hosts and kleptoparasites have cospeciated. This is the first clear evidence for the kind of host-symbiont cospeciation process which Platnick and Shadab (1978) suggested might have played a role in Mysmenopsis evolution. Presumably, the ancestral kleptoparasite species was fragmented into geographically isolated populations on Jamaica as a result of fragmentation of the host Ischnothele population, and each set of host/ kleptoparasite populations evolved independently in different environments under differing selection pressures.

The greater phenotypic difference (particularly in both male and female genital characters) between the two kleptoparasite sister species than between the two host sister species indicates that the former may have evolved more rapidly than the latter. Barnard (1984) lists four parameters which, if they differ between the host and parasite, may cause asymmetry in the rates of host and parasite evolution: population size, amount of variation within populations, the tendency of populations to become fragmented, and generation time. We lack enough information to evaluate the possible contributions of most of these and other factors to the apparently faster divergence of the Mysmenopsis populations, but we suggest that the probable difference in generation times between Mysmenopsis and Ischnothele could be one important factor. Like other tiny araneomorph spiders, these Mysmenopsis species probably have a generation time of no more than one year. Our observations of laboratory growth rates and size frequency distributions of Ischnothele species (including the Jamaican species) suggest that the Jamaican Ischnothele require 2 or 3 years to develop from egg to adult. Such a difference would mean a greater number of recombination and selection bouts per unit time in the Mysmenopsis populations than in the host Ischnothele populations; this would favor faster evolution of the kleptoparasite than the host.

## Ischnothele reggae, new species

Figs. 1-4, 7-13, 18, 20, 22, 24, 25, 27-29
Types.-Male holotype and 12 female paratypes from roadbanks in humid montane forest along road between Newcastle ( 3800 ft . elev.) and Hardwar Gap ( 4000 ft. elev.), St. Andrew Parish, Jamaica (8 April 1988 [male molted to maturity on 24 April 1988]; F. Coyle, R. Bennett, and A. Robinson), deposited in the American Museum of Natural History.

Etymology.-The specific name is a noun in apposition taken from a popular genre of Jamaican folk music.

Diagnosis.- The two known males of I. reggae can be distinguished from the three known males of $I$. xera by the following differences: 1) The tibia I apophysis is shorter (Figs. 9, 12, 13) (TAL $=0.11-0.12$ ) and wider ( $\mathrm{TAW}=0.23$ 0.27 ) [TAW $(100) /$ TAL $=193-243]$ than in $I$. xera (Figs. 9, 14-17) [TAL $=0.26$ 0.41 ; $\mathrm{TAW}=0.17-0.19$; $\mathrm{TAW}(100) / \mathrm{TAL}=45-64]$. 2) There are fewer prolateral spines on tarsus I (0-1) (Fig. 18) than in I. xera (2-4) (Fig. 19). 3) The two
prolateral spines on the pedipalp patella are much more slender and gradually tapering (Fig. 25) than in I. xera (Fig. 26), in which the more proximal of these spines is especially stout and tapers abruptly to an extremely thin deciduous tip. 4) The ocular quadrangle is proportionally wider [OQW(100)/CL $=28$-29] (Fig. 10) than in I. xera $[\mathrm{OQW}(100) / \mathrm{CL}=24-25]$. 5) The carapace edge setae are proportionally shorter $[\mathrm{CS}(100) / \mathrm{CW}=14-15]$ than in I. xera $[\mathrm{CS}(100) / \mathrm{CW}=18$ 22]. 6) Dorsal coloration is darker (Figs. 3, 8) than in I. xera (Figs. 5, 8).

Most females of I. reggae can be distinguished from those of I. xera by the following differences: 1) Since the ocular quadrangle is usually proportionally wider (Fig. 10) and the terminal article of the lateral spinneret is usually proportionally shorter than in I. xera, OQW(100)/LSL3 is the best ratio character for separating I. reggae (23-32) from I. xera (18-24) (Fig. 11). 2) CRT is usually greater ( $9-12$ ) than in I. xera (7-9). 3) Because of their relatively high CTR and relatively low ITarS, I. reggae females usually have a lower value for ITarS(100)/CTR (17-67) and a higher value for AMD(100)/ITarS (3.5-9.6) than do $I$. xera females (56-157, 1.9-3.8, respectively). 4) Dorsal coloration is usually darker than in I. xera (Figs. 4, 6, 8).

Males.-Table 1. Palpus (Figs. 20, 22, 24) with large bulb rather clearly delimited from embolus base; ventral face of bulb-embolus junction only slightly indented; terminal one-third of embolus slender in lateral view, curved upward and retrolaterally, with abrupt downward bend just short of tip, with serrations along retrolateral aspect of dorsal surface. Pedipalp tibia (Fig. 20) subcylindrical with only slight ventral swelling in proximal half; no enciform spines. Spines on dorsal aspect of prolateral face of pedipalp patella slender, long, and gradually tapering (Fig. 25). Tibia I apophysis (Figs. 12, 13) short, broad, with numerous apical spines ranging from short to very long. Proximal one-third of metatarsus I (Fig. 12) with strong ventro-retrolateral depression delimited distally by prominent ventro-retrolateral protuberance associated with more prolateral ventral keel; distal end of metatarus with ventral keel. Tarsus I flexible because of weakly sclerotized transverse "seams" over distal two-thirds (Fig. 18). Fovea a deep strongly procurved groove. One pair of long foveal setae. Bristles around lateral edges of carapace moderately long. Carapace pale yellow to orange yellow; chelicerae, pedipalps, and legs slightly darker. Abdominal dorsum with dark brown background color and 5-6 pairs of light areas; anterior pair largest, oval, joined by median pale area, other pairs (proceeding from anterior to posterior) progressively smaller, more obliquely transverse, more nearly united medially (Fig. 3). White setae not abundant.

Females.--Table 2. Spermathecae with two widely separated primary bulbs on each side and third, smaller, secondary bulb attached to (usually) or near lateral bulb (Figs. 27-29). Bulbs usually without stalks, heavily sclerotized; stalk, if present, short. Median bulb large, as tall or nearly as tall as lateral bulb. Fovea a deep strongly procurved groove (Fig. 1). One pair of long foveal setae (Figs. 1, 2). Bristles around edge of carapace moderately long (Fig. 1). Carapace pale yellow to orange-tan, similar to pedipalps and legs, lighter than chelicerae. Abdominal dorsum with medium to dark brown background color and 5-6 pairs of light areas as in males (Figs. 1, 4). White setae not abundant.

Variation.-See Analysis of Variation section above.
Natural history.--The I. reggae population observed between Newcastle and Hardwar Gap in the Blue Mountains favors road and trail banks in, or adjacent
to, moist forest. These banks range from low pebbly soil banks to high rock banks, some of which are exposed and considerably drier than others. Webs are abundant, reaching densities as high as five webs per $\mathrm{m}^{2}$ on two different sections of tall roadbank. Collecting labels indicate that webs are sometimes constructed in bromeliads. The tubular silk retreats penetrate rock crevices, drill holes, soil cavities, moss, and leaf litter, and open out via one or two tubular access passageways onto exposed capture webs composed of one or two roughly horizontal sheets plus other non-horizontal sheets and strands (sometimes including vertical strands up to 30 cm long) anchored to surrounding substrates. A typical I. reggae web has a horizontal capture area of about $400 \mathrm{~cm}^{2}$, but this value ranges up to $1200 \mathrm{~cm}^{2}$ in the largest webs.

The prey and prey capture behavior of I. reggae are described and discussed elsewhere by Coyle and Ketner (in press). In the field, these spiders appeared to be more reluctant to capture prey during the daytime than were other species of Ischnothele observed by the first author. I. reggae individuals run extremely fast (Coyle and Ketner in press) and/or feign death when forced out of their webs onto the ground; this plus their cryptic coloration makes them especially difficult to collect. Mysmenopsis monticola kleptoparasites were found in many of the larger I. reggae webs (Coyle and Meigs 1989).

Oviposition was observed in March, April, and May, but may not be limited to that period (A large number of third postembryonic instar spiderlings were collected with a female on 4 October 1957). As in the diplurid genus Euagrus (Coyle 1988), the bright white silk egg sac resembles a shallow silken bowl or short hammock holding the flattened spherical egg mass and covered with a layer of silk. It is usually suspended in the wall or floor of the tubular silk retreat. The I. reggae female tends to rest on the flat top of her egg sac (which is about as long as her body) or at least close to it, with her legs touching it. Of four egg sacs collected on 8 April, one contained only eggs, one contained only spiderlings in the second postembryonic instar (see Galiano 1972 for a description of postembryonic development in Ischnothele siemensis), one contained only fully active and pigmented spiderlings in the third postembryonic instar which appeared ready to abandon the egg sac, and one had recently been evacuated. Time from oviposition to evacuation of the egg sac ranged from 2.5 to 4 weeks in the seven broods produced in captivity. Brood sizes of the eight complete broods collected ranged from 47 to 100 and averaged 75.0. The three field-collected broods averaged larger $(63-100 ; 85.6)$ than the five broods produced in captivity (47-100; 68.6). Within the first week after evacuating the egg sac, third postembryonic instar spiderlings did not capture prey (Drosophila) while in their mother's capture web even though they could move about quickly and spin silk. However, when such spiderlings were placed in individual containers, they constructed webs and captured and ate Drosophila.

Distribution.--Known from elevations above 1700 ft . in the Cockpit Country of western Jamaica and above 3200 ft . in the Blue Mountains of eastern Jamaica (Fig. 7).

[^0](IJ); Cinchona Plantation, road to Morce's Gap, 4000 ft. elev., 22 March 1940 (C. B. Lewis), 1 female (IJ); Clydesdale, 3500 ft . elev., 7 June 1948 (D. E. Miller), 1 female (AMNH); vicinity of Morce's Gap above Clydesdale, 4800 ft. elev., in bromeliads, 19 June 1948 (C. J. Goin), 1 female, juvs. (AMNH); just W of Silverhill Gap, $3250-3500 \mathrm{ft}$. elev., in bromeliads, 9 July 1952, 1 female, 1 male, juv. (AMNH); Yallahs River above Silverhill Factory, in bromeliads, 1 July 1952, juvs. (AMNH). ST. THOMAS PARISH; Farm Hill Gap, circa 4000 ft . elev., sheet web with funnel retreat in earth bank, 1 May 1950 (G. R. Proctor), 1 female (IJ); Whitfield Hall, 4200 ft . elev., under stones, 13 April 1950 (R. P. Benpry), 3 females, juv. (IJ). TRELAWNY PARISH; Burnt Hill, 1700-2000 ft. elev., under rocks, 21 July 1985 (G. B. Edwards), 1 female (FSC).

Ischnothele xera, new species
Figs. 5-11, 14-17, 19, 21, 23, 24, 26, 30-35
Types.-Male holotype and one male and four female paratypes from cactus thorn scrub at Fort Clarence (20-100 ft. elev.) and adjacent part of Hellshire Hills (20-200 ft. elev.) near Seafort, St. Catherine Parish, Jamaica (9 April 1988 [paratype male molted to maturity in Oct. or Nov. 1988]; F. Coyle, R. Bennett, B. Freeman, and A. Robinson), deposited in the American Museum of Natural History.

Etymology.--The specific name refers to the arid nature of this species' habitat.
Diagnosis.-Refer to the diagnosis for I. reggae.
Males.-Table 1. Palpus (Figs. 21, 23, 24) with large bulb sharply delimited from embolus base (ventral face of bulb-embolus junction strongly indented); terminal one-third of embolus slender in lateral view, curved upward and retrolaterally, with abrupt downward bend just short of slender tapered tip, with serrations along retrolateral aspect of dorsal surface. 0-1 enciform spines on prolateral and retrolateral surface of cymbium near tip. Pedipalp tibia (Fig. 21) subcylindrical with only slight ventral swelling in proximal half; no enciform spines. Spines on dorsal aspect of prolateral face of pedipalp patella basally thick; proximal spine especially thick, tapering suddenly to extremely thin deciduous tip (Fig. 26). Tibia I apophysis (Figs. 14-17) long, relatively slender, with few to many apical spines ranging from short to very long. Proximal one-third of metatarsus I (Figs. 14, 16) with strong ventro-retrolateral depression delimited distally by prominent ventro-retrolateral protuberance associated with more prolateral ventral keel; distal end of metatarsus with ventral keel. Tarsus I flexible because of transverse weakly sclerotized "seams" over distal two-thirds (Fig. 19). Fovea a deep strongly procurved groove. One pair of long foveal setae. Bristles around lateral edges of carapace very long. Carapace pale yellow to orangeyellow; recumbent white setae abundant (Fig. 5). Chelicerae, pedipalps, and legs similar to carapace. Abdominal dorsum with light to medium brown background color and 5-6 pairs of light areas; anterior 2 pairs largest, oval, joined by median pale area, other pairs from anterior to posterior progressively smaller, more obliquely transverse, more nearly united medially; numerous recumbent white setae (Fig. 5).

Females.-Table 2. Spermathecae (Figs. 30-35) with two widely separated primary bulbs on each side, usually with third smaller secondary bulb which may or may not be attached to lateral bulb. Bulbs usually without stalks; stalk, if present, short. Median bulb varies from low (much shorter than lateral) and weakly sclerotized to larger (nearly as tall as lateral) and moderately heavily sclerotized. Fovea a deep strongly procurved groove. One pair of long foveal
setae. Bristles around edge of carapace very long. Carapace pale-yellow to orange-tan; recumbent white setae usually abundant peripherally and sometimes elsewhere on carapace (Fig. 6). Pedipalps and legs similar to carapace, chelicerae darker. Abdominal dorsum (Fig. 6) with light grey-brown to medium brown background color and pattern of 5-6 pairs of light areas as in males; recumbent white setae numerous to abundant.

Variation.-See Analysis of Variation section above.
Natural history.-The populations studied west of Kingston live in hot, dry, cactus thorn scrub on honeycombed limestone substrate with very little soil. Webs are usually found where retreat tubes can penetrate the otherwise sparse leaf litter that accumulates at the bases of rocks and in some of the holes and crevices in the soild rock substrate. The population studied east of Kingston lives in dry limestone forest on a rocky hillside and is much denser than the population west of Kingston. The webs are most often at the bases of rocks, trees, and exposed roots and their retreats penetrate the loose limestone pebble substrate. Ischnothele xera webs are similar in shape to those of I. reggae, but tend to be smaller.

Prey capture behavior is described by Coyle and Ketner (in press). Ischnothele xera, like $I$. reggae, is reluctant to capture prey in daylight, is extremely fast, and sometimes feigns death when forced out of the web onto the ground. Mysmenopsis furtiva kleptoparasites were found living in the webs of adult $I$. xera (Coyle and Meigs 1989).

The adult male collected on 9 April west of Kingston was in the retreat of what appeared to be his own functional capture web. Four I. xera broods were collected on 9-10 April: one egg sac contained only spiderlings still in embryonic cuticle with split and wrinkled chorions still attached, one sac contained active third postembryonic instar spiderlings which were about to emerge from the sac, and two recently emerged and fully active third instar broods were found in their mothers' retreats. These stages conform to the pattern of early postembryonic development described by Galiano (1972) for Ischnothele siemensis. One I. xera female oviposited in captivity on 10 May. The two complete $I$. xera broods collected (both from the population east of Kingston) are larger (125 and 137) than all eight known I. reggae broods (47-100).

Distribution.-Known only from two areas of low elevation along the south coast of eastern Jamaica (Fig. 7).

Material examined.-The type specimens and the following: JAMAICA: ST. CATHERINE PARISH: Port Henderson Hill, 250-500 ft. elev., 21 August 1952 (G. Underwood), 1 female (MCZ). ST. THOMAS PARISH; route A4, $14-15 \mathrm{mi}$. E Kingston, about 300 ft . elev., dry limestone forest, 10 April 1988 (F. Coyle, R. Bennett, B. Freeman, and A. Robinson), 1 female, juvs. (AMNH); 14 mi E Kingston, Morant Bay Road, below 250 ft . elev., 4 October 1957 (A. Chickering), 1 female, 1 male, juvs. (MCZ); 12 mi. E Kingston, about 200 ft . elev., 11 November 1957 (A. Chickering), 1 female (MCZ).

## Note added in proof:

Three males, two from the I. reggae type locality and one from the I. xera type locality, have recently matured in our laboratory. With the following three exceptions, their character states lie within the ranges of the diagnostically useful characters of the previously studied conspecific samples: 1) The tibia 1 apophyses of the new I. reggae specimens are longer (TAL $=0.14$ and 0.18 mm ) and narrower (TAW $=0.22$ and 0.20 mm ), and thus the TAW (100)/TAL values are considerably lower (160 and 116) than in the two conspecifics. 2) OQW(100)/CL
for the $I$. xera specimen is 26 , which is slightly higher than that of its three conspecifics. 3) Two of the new males have similar $\mathrm{CS}(100) / \mathrm{CW}$ values (I. reggae $=16.7$, I. xera $=17.3$ ) which lie between the ranges of the two previously described species samples. These new data reduce the usefulness of two of the seven diagnostic characters that separate the males of I. reggae and I. xera, however they are consistent with the hypothesis that these are different species.

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[^0]:    Material examined.-The type specimens and the following: JAMAICA: PORTLAND PARISH; 17 mi . post, Blue Mountains, tree bases, 28 July 1955 (A. F. Archer and T. H. Farr), 1 female (IJ); Green Hills, 3750 ft. elev., 10 Sept. 1950 (Sibley), 1 female, juvs. (IJ); Hardwar Gap, 4000 ft. elev., 27 June 1954 (A. Chickering), 4 females, juvs. (MCZ). ST. ANDREW PARISH; Catherine's Peak, 5000 ft. elev., 26 June 1936, 1 female (USNM); between Catherine's Peak and Newcastle, road to Clifton Ht., 4000 ft. elev., 16 July 1950, juvs. (IJ); Cinchona, 4000 ft. elev., Jan. 1912 (C. T. Brues), 2 females

